ENVIRONMENTAL CONTROL OF THE LOCAL-SCALE DISTRIBUTION OF FUNNEL ANTS, *APHAENOGASTER LONGICEPS*

A.O. NICHOLLS AND N.J. MCKENZIE

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Aphaenogaster longiceps, the funnel ant, is widespread in southern Australia. The genus is generally regarded as being more common on, or confined to, sandy soils ranging from the inland to the coastal forests. In this paper we model the effect of site, soil and vegetation characteristics on the probability of occurrence of nests of *A. longiceps*. The relative strength of the environmental variables in predicting the presence of nests of *A. longiceps* within a 20ha site in SE New South Wales is described. Aspect and topographic position are better predictors of nest occurrence than are surface soil texture (percent gravel and percent sand) or vegetative characteristics. The models are used to predict the likely response of *A. longiceps* to forest habitat fragmentation in eucalypt forest in SE New South Wales. ☐*Hymenoptera, Formicidae, funnel ant, Aphaenogaster longiceps, species distribution, statistical modelling, logistic regression, habitat fragmentatio, Wog Wog, Australia.*

A.O. Nicholls, CSIRO, Division of Wildlife and Ecology, PO Box 84, Lyneham, A.C.T. 2602; N.J. McKenzie, CSIRO, Division of Soils, GPO Box 639, Canberra, A.C.T. 2601; 29 July 1993.

The impact of forest habitat fragmentation on the ground dwelling arthropod fauna of a eucalypt forest is currently being studied at Wog Wog, SE New South Wales (Margules, 1992). The primary objectives of this experiment are to test predictions that flow from MacArthur & Wilson's (1967) equilibrium theory of island biogeography. The theoretical background, experimental design, sampling stratification and theoretical predictions are described by Margules (1992). In brief, there are two predictions of importance: the first is that habitat fragmentation reduces diversity and second that the reduction in diversity is dependent upon the fragment size (Margules, 1992). The major emphasis of the experiment is on the ground dwelling arthropod fauna. Herbage and understorey layers are also being monitored (Austin & Nicholls, 1988; Margules, 1992) to document their dynamics following habitat fragmentation and for the potential influence they might have on the distribution and abundance of the sampled fauna.

Funnel ants, *Aphaenogaster* spp., are known for their habit of creating widespread surface soil disturbance in association with their nest entrances (Sloane & Sloane, 1964; Saunders, 1967; Andersen, 1991). They can be a conspicuous component of the ground dwelling fauna and can influence the dynamics of the ground layer vegetation (Saunders, 1967). The presence of the nests of *A. longiceps* was recorded as part of the characterisation of the permanent monitoring sites in the Wog Wog experiment. The nests did not seem to be randomly distributed with respect to other site environmental variables.

The preference of *Aphaenogaster* spp. for selected habitats has been noted before (Saunders, 1967; Andersen, 1991); it is generally observed that *Aphaenogaster* spp. prefer sandy soils. Although there has been only limited work on habitat preferences of Australian ants there is clear evidence that ants can show affinities for selected soil types (Greenslade, 1976, 1987), aspects (Greenslade, 1985) and can partition the habitat in terms of rainfall gradients (Greenslade, 1974, 1976, 1987).

The objective of the present paper is to develop and describe correlative models relating the presence of nests of *A. longiceps* to a range of environmental variables that potentially represent different sources of control of the distribution of the species. These models will be used to predict the likely impact of forest fragmentation on this conspicuous component of the ground dwelling arthropod fauna.

METHODS

In 1987 an environmental survey of the 144 permanent sampling points within the Wog Wog

TABLE 1. Variables recorded for each permanent monitoring site grouped into three broad categories. Categorical variables or factors are indicated by the number of levels within brackets. Soil colour was recorded using the Munsell Color Company (1971) hue, value, chroma notation; electrical conductivity (EC) in a 1:5 water solution. Organic carbon is abbreviated as OC.

Topographic	Edaphic	Vegetational
Slope	A horizon	% Bare ground
Aspect	% Sand	% Litter cover
Landform(9)	% Clay	(leaves, bark,
Habitat(2)	% Gravel	grass, logs)
Catchment size(4)	Colour	% Shrub cover
Fire History(3)	Thickness	(*Kunzia*, *Acacia*,
Water Erosion(2)		*Eucalyptus*, other)
	B horizon	% Grass cover
	% Sand	% Herb cover
	% Clay	% Cryptogam cover
	% Gravel	(moss, lichens)
	Colour	% Cover ferns
		% Canopy cover
	EC	(*Eucalyptus*,
	pH	*Acacia*)
	Organic Carbon	

habitat fragmentation experiment was carried out just prior to the clearing of the surrounding forest. Variables were recorded in three broad classes; topographic, edaphic and vegetational (Table 1). Each permanent monitoring site consists of two 3×3m quadrats, separated by distances that varied from two to about four metres, on which most vegetational variables were recorded. The only vegetational characteristics not measured on these quadrats were the canopy cover of *Eucalyptus* spp. and *Acacia* spp., which were estimated for a 10×10m quadrat centred on a soil auger hole placed between the two 3×3m quadrats. Edaphic data were collected from this auger hole and associated samples submitted for laboratory analysis. Topographic data were recorded from the same location as the edaphic data. Presence or absence of nests of *A. longiceps* were recorded for each 3×3m quadrat.

The relationship between the presence or absence of nests of *A. longiceps* and the different suite of environmental variables was determined by fitting a statistical model — a multivariate logistic regression, from the class of regression models known as generalised linear models (McCullagh & Nelder, 1989). Numerous examples of the application of logistic regression models to demonstrate the relationship between the presence or absence of a species and a suite of environmental variables have been published for both plant species (Austin et al., 1983, 1984, 1990; Nicholls, 1989) and animal species (Adler & Wilson, 1985; Lindenmayer et al., 1991a, 1991b). Models were developed using the forward stepwise variable selection strategy outlined by Nicholls (1989) for predicting the probability of occurrence of *Eucalyptus radiata* as a function of a set of climatic, topographic and geological variables. The presence of a monotonic response as opposed to a unimodal response in each continuous variable was tested by fitting and comparing both first and second order polynomial functions.

A separate model was developed to estimate the probability of nest occurrence as a function of the variables belonging to each of the classes listed in Table 1. This permits an intuitive approach to evaluating the relative strength of the three models while permitting one to look at the variables that are correlated with the presence of *Aphaenogaster* nests. A more formal approach to this relative evaluation would be to use the forward selection procedure across all variables from all three classes. The usual set of regression diagnostics, techniques developed to assist with the evaluation of the assumptions implicit in fitting regression models to data, were applied to the final models to assess observations not well fitted by the model (outliers) and observations with undue or potential influence on the parameter estimation (Nicholls, 1989; Hosmer & Lemeshow, 1989; Collett, 1991).

MODELS FOR INDIVIDUAL CLASSES OF VARIABLES

TOPOGRAPHIC VARIABLES

A number of variables showed significant relationships when tested singly. Of these the following were the most important: aspect, the experimental design factor habitat (slope or drainage line), catchment size and landform (Table 2). The variables — habitat, landform and catchment size — produced a significant improvement when added to a model with aspect (Table 3). The variables slope and landform produced significant improvement in a model including aspect and habitat. Of these, slope was the most important and was added to the model.

TABLE 2. Changes in deviance (a measure of the lack of fit used to assess logistic regression models fitted to binary data) when the topographic variables were fitted singly to the null model. This table represents the results of the first pass of the forward stepwise fitting procedure.

Variable	d.f.	Deviance	d.f.	Deviance	P
Null	287	213.09			
Slope	286	212.68	1	0.412	>0.1
Slope+Slope^2	285	211.59	1	1.097	>0.1
Aspect	286	181.80	1	31.294	<0.001
Aspect+Aspect^2	285	178.45	1	3.353	0.067
Landform	279	180.51	8	32.582	0.001
Habitat	286	194.55	1	18.544	<0.001
Catchment size	284	193.19	3	19.904	<0.001
Fire History	285	210.02	2	3.081	>0.1
Water Erosion	286	208.27	1	4.822	0.028

Subsequent testing of the remaining variables produced no further significant reduction in the deviance. Thus a three variable model proved to be an adequate model. The regression coefficients for this model are given in Table 4 and the model displayed in Fig. 1. Interpretation of the regression coefficients is as follows: the positive coefficient for aspect indicates an increasing probability of finding a nest as the aspect increases towards 360°, the negative coefficient for slope reflects a declining probability of nest occurrence on flatter sites compared to sites on slopes. The habitat coefficient is the difference between the two predicted surfaces defined by aspect and slope and reflects a 3.5 times decline in the ratio of the odds (presence/absence) of a prediction for a drainage site compared with a comparable slope site. Figure 1 shows the distribution of the observations in the multidimensional space defined by slope and aspect. The lines show where in that two dimensional space the model predicts selected probabilities of nest occurrence for given combinations of slope and aspect. Note that a predicted probability of 0.1 implies that for ten sites (for example slopes) with the same slope and aspect, one would expect one site to have *Aphaenogaster* nests; in contrast for a predicted probability of 0.5, five of the ten sites would be expected to have nests.

EDAPHIC VARIABLES

Textural variables, percent sand, gravel or clay for the A1 horizon or the B horizon showed a significant relationship with the presence of *A.*

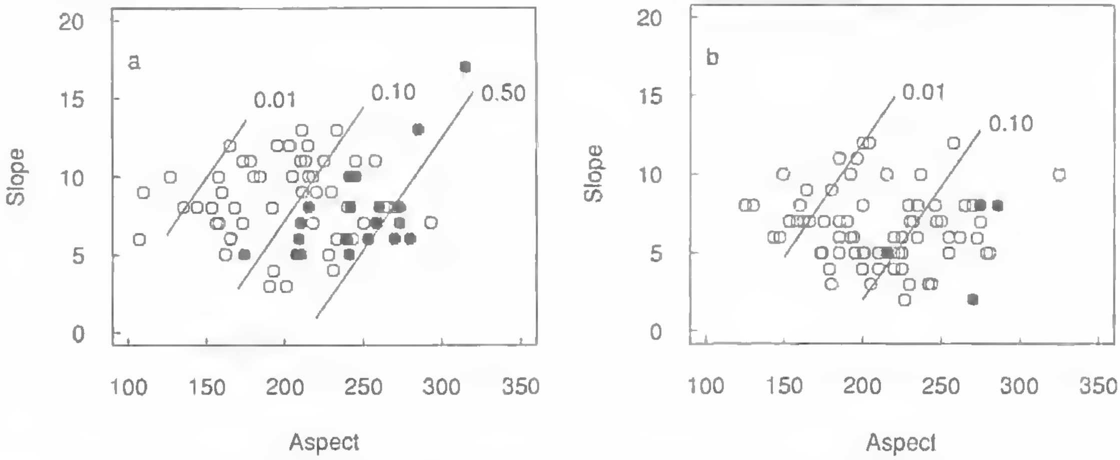

FIG. 1. Observed and predicted probabilities of occurrence of nests of *A. longiceps* as a function of aspect, expressed as degrees from north, for sites classified in the field as either slopes (a) or drainage lines (b). Sites are shown as solid symbols where nests were present and as open symbols where absent. Continuous lines show the predicted probability of nest occurrence.

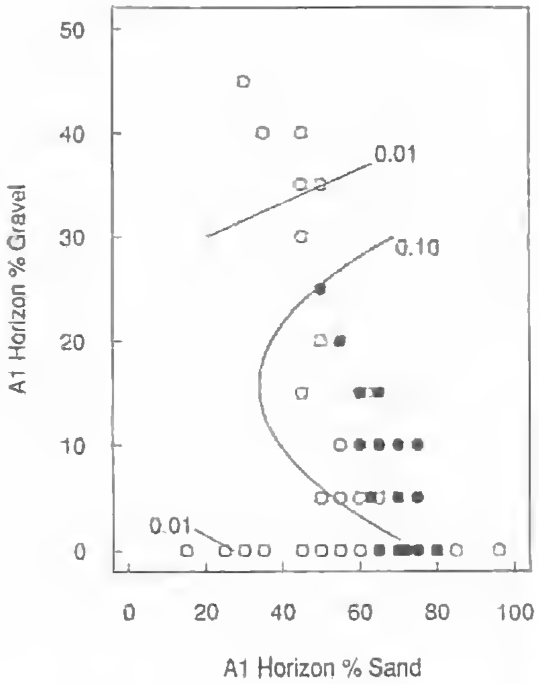

FIG 2. Distribution sites in the environmental space defined by percent gravel and percent sand. Sites are shown as solid symbols where nests were present and as open symbols where absent. Continuous lines show the predicted probability of nest occurrence.

longiceps nests (Table 5). The colour, expressed as the chroma (Munsell Color Company, 1971), of the A2 and B horizons showed less pronounced but significant relationships (Table 5). The final model was a quadratic function of the percent gravel of the A1 horizon plus a linear function of the percent sand of the A1 horizon (Table 6). For any given values of percent sand the maximum predicted probability of occurrence will be at about 15-16% gravel content. The predicted surface and observed data are shown as a function of these two variables (Fig. 2).

VEGETATIONAL VARIABLES

The vegetational characteristics fall naturally into three groups: litter, understorey components and the canopy. Significant relationships were found for litter and understorey components but not for canopy components (Table 7). Percent bare ground was the most significant litter component whereas percent grass cover was the most important single variable of the understorey group (Table 7). The selected model was a quadratic function of percent bare ground, linear function of percent moss cover and a linear function of percent grass cover (Table 8). Maximum probabilities are predicted for percent bare ground around 15%; the probability of occurrence declines with increasing cover of grass and moss. For moss cover the rate of decline of the odds ratio is about 1.6 times that for grass cover.

COMPARISON OF THE THREE MODELS

The three models can be compared informally in terms of the overall measure of lack of fit. For generalized linear models, this measure is usually referred to as the deviance (McCullagh & Nelder, 1989). Although for many generalized linear models the behaviour of the deviance is understood for models based on binary (that is presence or absence) data (such as used here) the behaviour is known not to have expected asymptotic properties. For this reason the use of the deviance as a measure of model adequacy is not recommended (McCullagh & Nelder, 1989). However, we can use it to rank the three final models: the topographic model had a residual deviance of 152 with 284 degree of freedom; the vegetation model a deviance of 168 with 283 degrees of freedom; and the soil-based model a deviance of 190 with 284 degrees of freedom. The topographic-based model offers the greatest explanation of the observed variation in distribution of nests of *A. longiceps* and the vegetation model the least explanation.

DISCUSSION

Despite the rarity of occurrence of nests — present on 35 of the 288 quadrats (which were located on 25 of the 144 sites) — a wide range of environmental variables drawn from the three classes have significant relationships with the occurrence of *A. longiceps* nests (Tables 2, 5 & 7). This result reflects the likely collinearity of many of the environmental variables within the sample of sites used for monitoring the impact of fragmentation. Despite this, it is possible to draw some conclusions about the influence of environment on the distribution of *A. longiceps* within the local region of the Wog Wog habitat fragmentation experiment.

The site or topographic-based model demonstrates a clear preference of species for warm exposed (north-west facing) slopes (Fig. 1). In addition, the preference for sandy soils on warm slopes suggests that this species avoids wet conditions. As noted by Margules (1992) the

TABLE 3. Changes in deviance (a measure of the lack of fit used to assess logistic regression models fitted to binary data) when the topographic variables were added singly to the model containing the linear function on aspect. This table represents the results of the second pass of the forward stepwise fitting procedure.

Variable	d.f.	Deviance	d.f.	Deviance	P
Aspect	286	181.80			
+ Slope	285	180.30	1	1.502	>0.1
+ Slope+Slope^2	284	180.25	1	0.049	>0.1
+ Aspect+Aspect^2	284	178.45	1	3.353	0.067
+ Landform	278	147.07	8	34.730	<0.001
+ Habitat	285	160.99	1	20.815	<0.001
+ Catchment size	283	160.36	3	21.446	<0.001
+ Fire History	284	176.36	2	5.442	0.066
+ Water Erosion	285	176.90	1	4.898	0.027

TABLE 4. Regression coefficients and approximate standard errors for the final model relating probability of occurrence of nests of *A. longiceps* with selected topographic and site variables.

Variable	Parameter estimate	Standard error	t value	P
Intercept	-8.649	1.598	5.41	<0.001
Habitat	1.247	0.271	4.61	<0.001
Aspect	0.03468	0.00682	5.08	<0.001
Slope	-0.2407	0.0839	2.87	0.005

TABLE 5. Changes in deviance (a measure of the lack of fit used to assess logistic regression models fitted to binary data) when the edaphic variables were fitted singly to the null model. Textural components are abbreviated, sand = S, clay = C, and gravel = G. All continuous variables were fitted as both first and second order polynomial functions. Where no second order function is shown below it may be assumed that the change in deviance due to the addition of the quadratic term was not significant and was less than 2.

Variable	d.f.	Deviance	d.f.	Deviance	P
Null	287	213.10			
A horizon					
%S	286	209.60	1	3.49	0.062
%S + %S^2	285	204.54	1	5.06	0.024
%C	286	205.14	1	7.96	0.005
%C + %C^2	285	202.69	1	2.45	>0.1
%G	286	212.58	1	0.52	>0.1
%G + %G^2	285	194.48	1	18.09	<0.001
A2 horizon					
Thickness	286	213.10	1	0.00	>0.1
Colour					
Hue	286	212.30	1	0.80	>0.1
Hue+Hue^2	285	208.83	1	3.47	0.062
Value	286	212.06	1	1.04	>0.1
Chroma	286	204.69	1	8.41	0.004

TABLE 6. Regression coefficients and approximate standard errors for the final model relating probability of occurrence of nests of *A. longiceps* with selected edaphic variables. Residual deviance for this model was 190.05 with 284 degrees of freedom. Edaphic variables are abbreviated, % gravel as %G and % sand as %S.

Variable	Parameter estimate	Standard error	t value	P
Intercept	-5.9428	1.8491	3.21	0.002
A1 %G	0.2639	0.0680	3.88	<0.001
A1 %G + %G^2	-0.00844	0.00305	2.77	0.007
A1 %S	0.0496	0.0258	1.93	0.057

TABLE 7. Changes in deviance (a measure of the lack of fit used to assess logistic regression models fitted to binary data) when the vegetation variables were fitted singly to the null model. All continuous variables were fitted as both first and second order polynomial functions. Where no second order polynomial function is shown below it may be assumed that the change in deviance due to the addition of the quadratic term was not significant and was less than 2.

Variable	d.f.	Deviance	d.f.	Deviance	P
Null	287	213.10			
% Bare grnd	286	201.43	1	11.67	<0.001
% Bare grnd^2	285	188.94	1	12.49	<0.001
Litter					
% Leaf	286	212.29	1	0.81	>0.10
% Leaf^2	285	209.02	1	3.27	0.071
% Bark	286	209.57	1	3.52	0.061
% Bark^2	285	208.37	1	1.21	>0.10

TABLE 8. Regression coefficients and approximate standard errors for the final model relating probability of occurrence of nests of *A. longiceps* with selected vegetation variables.

Variable	Parameter estimate	Standard error	t value	P
Intercept	-1.2785	0.4434	2.88	0.004
% Bare ground	0.3249	0.1254	2.59	0.010
% Bare ground^2	-0.0110	0.0072	1.52	>0.10
% Moss	-0.0972	0.0428	2.27	0.024
% grass	-0.0596	0.0267	2.34	0.026

experimental site was selected such that the layout of the remnants was on a predominantly south western facing slope. Despite this, the local relief within the experimental site causes aspects for the 144 monitoring sites to range from 107° to 325° with the majority between 185° and 240°. There is little difference between those monitoring points classified as slopes and those as drainage lines in terms of the range of aspects nor in terms of their slope. There is little correlation between site aspect and slope (Fig. 1). The impact of fragmentation of the forest will not change the aspect or slope of the monitoring sites although the exposure of sites can increase due to the loss of surrounding forest canopy This can be most noticeable for sites close to the edges of the remnants and may change the range of effective exposure, increasing it for westerly aspects and perhaps decreasing it for southerly aspects. Given the preference of *A. longiceps* for nesting on westerly to north-westerly (=warm) sites and the potential for increased exposure following forest canopy fragmentation, the response of this ant to the direct impact of fragmentation will be to maintain or perhaps to increase its current rate of site occupancy.

The strong influence of surface texture on the probability of nest occurrence is consistent with the usual statements about the preference of *Aphaenogaster* spp. for sandy soils (Sloane &

Sloane, 1964; Saunders, 1967; Andersen, 1991). Although the best model includes the A1 horizon sand content, it also contains the gravel content of that layer, a point not noted in the literature. Neither of these two variables are likely to change dramatically due to the fragmentation treatment. The question of collinearity within the data matrix is important because the soils with high clay content tend to dominate the gullies. Total separation of the influence of surface texture from that of topography might not be possible without more extensive sampling. Although a formal test of the difference between the two models has not been undertaken, the site-based model appears to offer better predictive ability than the soil-based model.

The interpretation of the final vegetation-based model is less clear because more variables are included and these show more correlation than one would like when undertaking this type of modelling exercise because of the difficulty of separating the influence of individual variables when there is high collinearity. Also, these variables can themselves respond to the impact of fragmentation of the forest. Increased exposure — particularly around the edges and perhaps over all of the small remnants — may result in a loss of moss cover and a reduction in grass cover. This could lead to an increase in bare ground, one of the important predictor variables in this model. Such changes, if they occur, may lead to an increase in favourable nest sites because the probability of occurrence is negatively correlated with both moss and grass cover.

It should be noted that there are substantial differences in the distribution of moss cover on the slopes in contrast to the drainage lines. The inclusion of moss cover in the model as a predictor might be the result of this difference. Frequent and high moss cover is characteristic of drainage lines; as such, it may be acting as a surrogate for the habitat variable noted as an important predictor in the site-based model rather than the ants responding directly to the extent of moss cover.

On the basis of the three independently fitted models, the dominant influences on the distribution of nests of *A. longiceps* appear to be those that are not likely to change following the clearing of the surrounding forest to create habitat remnants. This suggests that the fragmentation treatment imposed on this eucalypt forest is unlikely to have a direct impact on the distribution of *A. longiceps* nests. This is not in conflict with the concern expressed by Sloane & Sloane (1964) with the impact of habitat loss on *A. longiceps*.

The prediction that fragmentation will not result in a reduced rate of site occupancy will be tested in two ways and the results reported elsewhere. A re-survey of the quadrats is planned for the spring or summer of 1993/94. This would be directly comparable to the 1987 survey and nest loss could be determined and related to the isolation treatment, habitat remnant size and position within the remnant. A second test of the prediction will be based on changes in distribution and relative population size of *A. longiceps* caught in pitfall traps operated quarterly for the duration of the experiment (Margules, 1992).

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